

Sclerobionts on biogenic substrates from the Monte León Formation (lower Miocene) in Santa Cruz Province, Argentina: Taphonomic and paleoenvironmental considerations

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ABSTRACT

Study of hard-substrate communities in a paleoenvironmental and taphonomic context contributes towards increasing knowledge on the depositional environments and on the history of the substrate colonized before final burial. In this work we study traces produced by sclerobionts on biogenic substrates from two shell concentrations in the Monte León Formation (lower Miocene), exposed at Cabeza de León, southern Patagonia, Argentina. The aims of this study are to describe the bioerosion traces and to infer the taphonomic history of the hard substrates (mollusk shells) based on ichnodiversity and sclerobiont distribution together with other preservational features. Fifteen ichnotaxa were identified at different taxonomic ranks (one ichnofamily, three ichnogenera and eleven ichnospecies). Traces produced by bryozoans were highly predominant followed by those produced by sponges, (?)foraminifera and polychaetes. The biogenic substrates on which the sclerobionts settled were gastropod and bivalve shells showing different taphonomic signatures. Shells with high fragmentation and surface-alteration are dominant, suggesting that they were reworked by wave action before deposition and final burial. On the other hand, well preserved shells reflect less reworking and shorter transport distance. The mixture of these elements could be the result of short-term high-energy events such as storms. Yet, these taphonomic signatures were modified later by biologic factors, mainly bryozoan bioerosion in a quiet and shallow environment with a low sedimentation rate and abundant nutrient availability. Bioerosion valuation in conjunction with other taphonomic attributes allowed identifying the concentrations as of mixed origin (biogenic-sedimentologic) and including elements that underwent different taphonomic histories. The results contribute to improve the knowledge about marine hard substrate communities in middle to high latitudes of the southern hemisphere. In addition, they highlight the importance of conducting studies on these communities –in conjunction with other taphonomic data– when elucidating the history of colonized substrates.

1. Introduction

Bioerosion is defined as biologic erosion on hard substrates performed by mechanical or chemical means (Neumann, 1966). For several years, paleontologists and neontologists have recognized the importance of the ecological and evolutionary information that marine hard substrate communities provide (e.g. Bingham, 1992; Wilson and Taylor, 2001; Taylor and Wilson, 2003; Wilson, 2007; Buatois et al., 2016; Zatón et al., 2016; Bassi et al., 2017). Taylor and Wilson (2002) established a terminology reflecting the relationship between the organisms and the substrate they occupy and proposed the term

sclerobiont to refer to any organism fouling any kind of hard substrate. It includes encrusters addressed closely to the surface of the substrate, sessile organisms that are cemented or organically anchored to the substrate surface but grow into the water column, borers that penetrate the substrate to different depths and vagile organisms living on or habitually visiting the substrate.

The study of marine hard substrate communities provides important paleoecological information such as life position of colonizers, and their distribution and spatial orientation on the substrate, and it also provides evidence of interactions between sclerobionts either as ecological succession or as competition (e.g. Wilson, 1985, 1987; Taylor and

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Wilson, 2003; Parras and Casadío, 2006; Brezina et al., 2014; Luci and Lazo, 2015; Färber et al., 2016; Liow et al., 2016; Taylor, 2016). In an evolutionary context, the study of these communities is interesting because different clades have developed this strategy throughout the Phanerozoic (Taylor and Wilson, 2003). Finally, in a taphonomic and paleoenvironmental context, the study of marine hard substrate communities increases the information about depositional conditions and taphonomic history of the colonized substrates before final burial (e.g. Siggerud et al., 2000; Domènech et al., 2001; Johnson et al., 2011; Pineda-Salgado et al., 2015).

The Monte León Formation (lower Miocene, Austral Basin, Santa Cruz, Argentina) contains numerous concentrations of fossil invertebrates (del Río, 2004; Parras and Griffin, 2009; Parras et al., 2012) that offer an excellent opportunity to study the biota associated with hard substrates. The aims of this work are to describe the bioerosion traces present in the biogenic substrates of two shell concentrations in this unit and to recognize what kind of information their richness, abundance and distribution provides in shells with different taphonomic attributes (i.e. fragmentation and surface alteration). The final aim is to recognize the biological and sedimentary processes that were responsible for the formation of the shell concentrations involved. This constitutes the first study of sclerobionts in the Monte León Formation within a sedimentological and taphonomical context, contributing to increase the available knowledge on marine hard substrate communities in this unit, as well as the composition of these communities in middle to high latitudes of the southern hemisphere. In addition, this study can be considered as another example of the importance of quantitative studies of sclerobiont communities in conjunction with other paleontological and taphonomic data of the preserved elements and biofabric analysis (sensu Kidwell et al., 1986) as a way of improving paleoenvironmental interpretations and reconstructions of the taphonomic history of fossil concentrations.

2. Geological setting

During the Late Cretaceous, Paleogene and Neogene, Patagonia was flooded by different Atlantic transgressions that deposited marine rocks now widely exposed mainly along the coast and along the foothills of the Andes. These rocks are intercalated with non-marine rocks or interrupted by periods of erosion or non-deposition. The transgression occurring during the late Oligocene and early Miocene is referred to as *Patagoniense*. In the Austral Basin the sedimentary rocks deposited during this transgression are exposed mostly along the coastline and in the Andean range sector. These rocks are included in the San Julián (Bertels, 1970) and Monte León (Bertels, 1970) Formations in the coastal region of Santa Cruz Province, and in the Estancia 25 de Mayo (Cutíño and Scasso, 2010) and El Chacay (Chiesa and Camacho, 1995) Formations in the Andean region. The Estancia 25 de Mayo Formation is exposed in the Lago Argentino area and the El Chacay Formation is exposed farther north in the Lago Posadas area. In Chile, equivalent rocks referred to the Guadal Formation (Niemeyer et al., 1984) are exposed in the Lago General Carrera area. In the San Jorge Gulf basin (Comodoro Rivadavia area) these deposits are included in the Chenque Formation (Bellosi, 1990).

The Monte León Formation (Bertels, 1970) includes yellowish-grey fine sandstones and siltstones with a high pyroclastic content. It crops out along the coastline of Santa Cruz Province and measures between 180 and 200 m thick (Panza et al., 1995). It unconformably overlies the late Oligocene marine San Julián Formation (Parras et al., 2008, 2012). Overlying the Monte León Formation is the Santa Cruz Formation, which includes early-middle Miocene continental deposits (Fleagle et al., 1995; Perkins et al., 2012). Bertels (1980) considered that the Monte León Formation was deposited in an outer shelf environment. Towards the top, the depositional conditions become progressively shallower and end in a marshy environment (Barreda and Palamarczuck, 2000; Panza et al., 1995). Parras and Griffin (2009)

suggested a depositional environment ranging from inner shelf to subtidal at the base, to intertidal towards the top at the mouth of the Río Santa Cruz. In relation to the pyroclastic material content, Bertels (1970) interpreted it as produced by volcanic events occurring towards the west in the Andes and transported to the shore by the predominant westerly wind.

The age of the Monte León Formation was at first estimated based on foraminifera and ostracods, suggesting that the unit had been deposited either during the late Oligocene (Bertels, 1970, 1980) or the middle Miocene (Becker, 1964). Later, palynology, calcareous microfossils (Barreda and Palamarczuck, 2000; Nández et al., 2009) and biostratigraphic analysis based on mollusks (del Río, 2004) dated the deposits of the Monte León Formation as early Miocene. Recently, Parras et al. (2012) obtained a series of ages based on strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) on calcitic shells collected in the unit. The ages ranged between ~22 and 18 million years (early Miocene, Aquitanian and Burdigalian stages). Perkins et al. (2012) using $^{40}\text{Ar}/^{39}\text{Ar}$ isotopes dated the overlying Santa Cruz Formation as 17.7 million years at the base. This age confirms the age estimated by Parras et al. (2012) for the top of Monte León Formation, restricting it to the early Miocene.

3. Study area and material

The samples studied come from the Cabeza de León section located in the Monte León National Park (Fig. 1), along the coastline of Santa Cruz Province (50° 21' 25.4" S; 68° 53' 05.9" W). The lower part of the section contains approximately 17 m of bioturbated siltstones and fine sandstones, massive or with horizontal stratification. Invertebrate fossils are scarce and are represented by articulated decapods and specimens of "*Ostrea hatcheri* Ortmann, 1897 in life position. The middle part of the section measures approximately 11 m thick and contains a highly bioturbated fine sandstone. In this sector there are many fossil concentrations including gastropods, bivalves, scaphopods, brachiopods, echinoderms, barnacles and bryozoans. Each concentration shows a distinctive taphonomic signature. The uppermost meters of the section include tuffaceous siltstones and fine sandstones with heterolithic bedding (Fig. 2A, B).

The studied material comes from a 1.3-m-thick bed containing fossiliferous lenses, one of them considered here as the first shell concentration (sample M1); and from a 0.5-m-thick continuous fossiliferous bed considered the second shell concentration (sample M2) (Fig. 2). Samples a and b from the second concentration were taken to test vertical variations within it (Fig. 2C). The shell concentration represented by M1 has a medium-grained sandstone matrix with lens geometry, dense packing and well sorted by size. Fragmentation is high and fossil orientation (mainly bivalves) is chaotic. The concentration represented by M2 (a and b) has a matrix of medium-grained bioclastic sandstone and bed geometry with wavy base and flat top; the packing is dense and size sorting poor. Bivalve shells with moderate fragmentation predominate in the base (M2a); their orientation is concordant to stratification, with upward convexity. Gastropod shells with random orientations are abundant towards the top (M2b).

4. Methods

4.1. Sample preparation, taphonomic attributes and sclerobionts

From each sample collected (M1, M2a and M2b) a volume equivalent to 1 l was quartered, washed and wet sieved with ZonyTest® sieves with mesh size $3^{1/2}$ (5.660 mm), 16 (1.190 mm) and 25 (0.710 mm). Only the shelly material retained in the first mesh was considered for this study. The material was observed under a Leica M80 stereoscopic microscope to identify the sclerobionts present and the degree of bioerosion.

Bioerosion was quantified as low, moderate and high according to the percentage of the shell surface that was affected: (1) low, when the

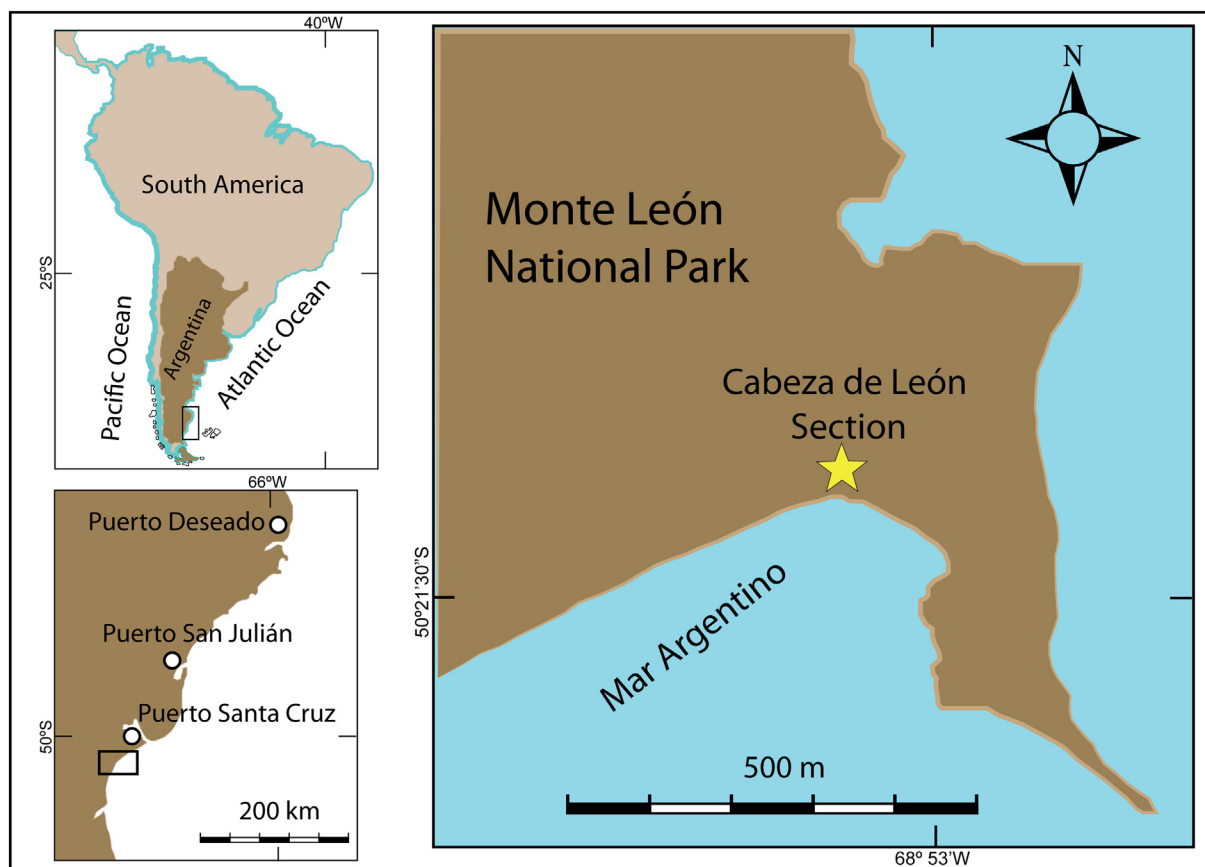


Fig. 1. Study area. Location of Cabeza de León, where the studied section is exposed.

shell surface affected was under 30%, (2) moderate, when the bioeroded surface ranged between 31 and 60%, and (3) high, when bioerosion traces covered over 60% of the shell surface. The ichnodiversity of each sample was also determined, as well as the relative abundance of each ichnotaxon. The recognized traces were identified to the lowest possible ichnotaxonomic rank. Even though predation drilling traces are considered as bioerosion traces, they were quantified separately using the presence-absence criterion; attack effectiveness was not considered. Traces were photographed with a Leica EC3 camera at the Universidad Nacional de La Pampa and with the SEM at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”.

In addition to the bioerosion traces, other taphonomic attributes were considered such as fragmentation and surface alteration. The degree of fragmentation was established considering the proportion of the shell preserved as (1) low, when between 100 and 70% of the shell is preserved, (2) moderate, when the proportion of the shell preserved is from 69 to 40%, and (3) high, when < 40% of the shell is preserved.

Due to the difficulty in recognizing the effects of dissolution and abrasion separately, these were considered jointly as surface alteration, being (1) low, for specimens with well-preserved ornamentation and/or polished appearance, (2) moderate, for those specimens with weathered ornamentation and/or opaque appearance, and (3) high, for the specimens that show holes produced by dissolution and a chalky appearance or those in which ornamentation is completely weathered. Only two edge modifications were considered, i.e. edges with notch by fragmentation and edges rounded or smooth by corrosion.

4.2. Treatment of data

All the revised specimens were included in a data base that, for each sample, includes the degree of bioerosion, fragmentation, and surface alteration as well as the presence-absence of drilling. The percentages

of each attribute were plotted.

To find out if each ichnotaxon was present on both surfaces of the shells or only on one of them a data base was assembled for each sample. Preferential settling on either surface (internal or external) was also recorded. Ichnotaxa recognized were associated to their possible producers to test by an Exact Goodness-of-Fit Test (with two tails and a confidence interval of 0.95) if traces of each producer were preferably located on both or just on only surface of the shells. In the latter case, the test was repeated to identify if there was a significant preference for the internal or external surface. As most of the shelly remains that conform the concentrations belong to organisms with infaunal or semi-infaunal life habits (see Results and Discussion) the null hypothesis considered was that the sclerobionts settled randomly on one or both surfaces of the shells, and also randomly on internal-external surface. Finally, to assess bioerosion for all the producers as a whole in each sample, a Fisher Test was performed in which the null hypothesis suggests that the producers colonized one or both surfaces of the shells in a random way. The tests were performed using R Studio software version 0.98.1103 (RStudio Team, 2015).

5. Results

5.1. Ichnotaxa

Fifteen ichnotaxa were recognized based on morphological criteria. One of these was identified only to the ichnofamily rank, three to ichnogeneric rank and eleven to ichnospecific rank. Most belong to the Domichnia ethological category.

Ichnodiversity was rather low in the first concentration, in which 12 ichnotaxa were recognized, while in the second concentration 14 were recognized in M2a and 13 in M2b (Table 1). Regarding the relative abundance of the ichnotaxa, those produced by bryozoans were

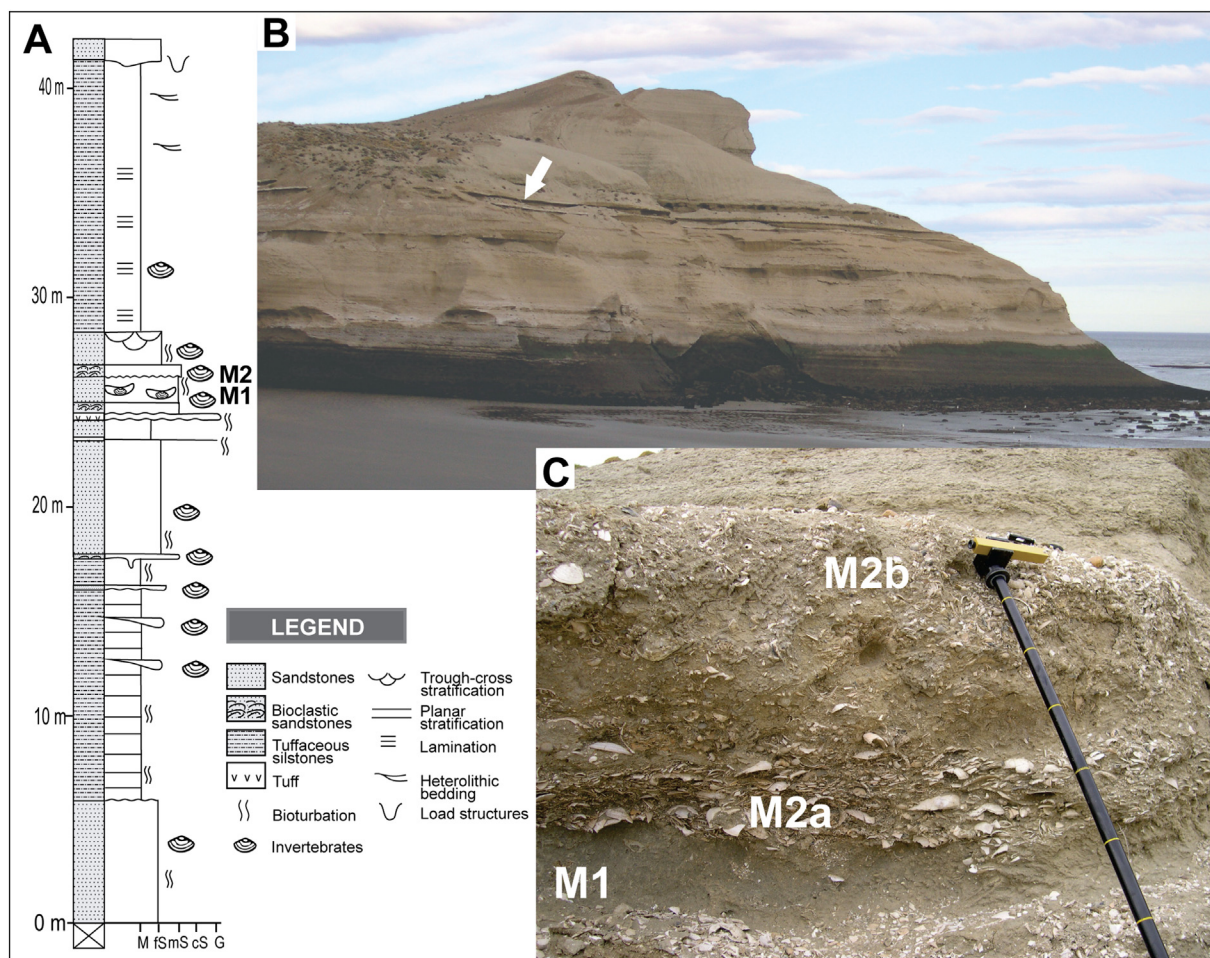


Fig. 2. A) Stratigraphic section of Monte León Formation at Cabeza de León locality with the location of the studied samples. B) General view of Cabeza de León section, showing different fossil concentrations; the white arrow indicates the sector where the samples came from. C) Detailed view of the studied shell concentrations, with the location of the studied samples (M1, M2a, M2b). Note the predominance of bivalve shells concordant to stratification, with upward convexity in the base of the second shell concentration (M2a) and of small gastropod shells with chaotic orientation towards the top (M2b).

Table 1
Ichnotaxa recognized in fossil shell concentrations of the Monte León Formation (Cabeza de León section) showing their presence in each sample. Also includes the possible producers of the traces and their ethology.

Ichnotaxa	Producer	Ethology	M1	M2a	M2b
<i>Caulostrepis biforans</i>	Polychaetes	Domichnia	X	X	X
<i>Caulostrepis taeniola</i>	Polychaetes	Domichnia		X	X
Dendrinidae	?Foraminiferans	Domichnia	X	X	X
<i>Entobia</i> isp.	Sponges	Domichnia	X	X	X
<i>Finichnus dromeus</i>	Bryozoans	Domichnia	X	X	X
<i>Finichnus peristroma</i>	Bryozoans	Domichnia	X	X	X
<i>Gastrochaenolites ornatus</i>	Bivalves	Domichnia			X
<i>Maeandropolydora sulcans</i>	Polychaetes	Domichnia	X	X	X
<i>Maeandropolydora</i> isp.	Polychaetes	Domichnia		X	
<i>Oichnus paraboloides</i>	Gastropods	Praedichnia	X	X	X
<i>Oichnus simplex</i>	Gastropods	Praedichnia	X	X	X
<i>Pennatichnus moguerenica</i>	Bryozoans	Domichnia	X	X	X
<i>Pennatichnus</i> isp.	Bryozoans	Domichnia	X	X	X
<i>Pinaceocladichnus onubensis</i>	Bryozoans	Domichnia	X	X	X
<i>Podichnus centrifugalis</i>	Brachiopods	Fixichnia	X	X	

predominant, representing in both concentrations an overall relative abundance of > 50% (Fig. 3). *Pennatichnus* Mayoral, 1988 was the most abundant ichnogenus, with a proportion between 26 and 28%. Samples M1 and M2a also have abundant traces of *Entobia* Bronn, 1873 and Dendrinidae, which together represent 34% and 29% respectively in each sample. Conversely, in sample M2b *Entobia* and Dendrinidae

together represent only 7% of all traces. Traces produced by polychaetes (*Caulostrepis* Clarke, 1908 and *Maeandropolydora* Voigt, 1965) in M1 and M2a were scarce, reaching 9 and 13% while in M2b they represented 20% of the sample. In the three samples, the abundance of *Maeandropolydora* was greater than *Caulostrepis*. Finally, the traces that correspond to the ethological categories Praedichnia and Fixichnia were very scarce; in M1 and M2a *Oichnus* Bromley, 1981 was < 4%, while in M2b it was 14%; in this case the percentages of *O. simplex* Bromley, 1981 and *O. paraboloides* Bromley, 1981 were similar. Traces of *Podichnus* Bromley and Surlyk, 1973 were present only in M1 and M2a with a percentage of 2% or less.

Ichnogenus *Caulostrepis* Clarke, 1908

Ichnospecies *Caulostrepis biforans* (Gripp, 1967)

Material. Trace bent in a narrow U with a length between 3 and 4 mm and average width of 1 mm (Fig. 4A). Vane absent. Limbs not fused but closely merged by an intermediate wall, their width between 0.34 and 0.42 mm near the aperture and between 0.40 and 0.55 mm near the base of the trace. Transverse section is circular to oval. The preservation of the traces varies; in some cases, the gallery is not complete due to fragmentation or surface alteration which also can affect the preservation of the intermediate wall. Apertural grooves absent.

Remarks. These traces were assigned to *Caulostrepis* due to the U-shaped gallery, while the absence of the vane and the transverse section allow the ichnospecific assignment. They are different from *C. avipies* Bromley and D'Alessandro, 1983, because *C. avipies* shows a transverse

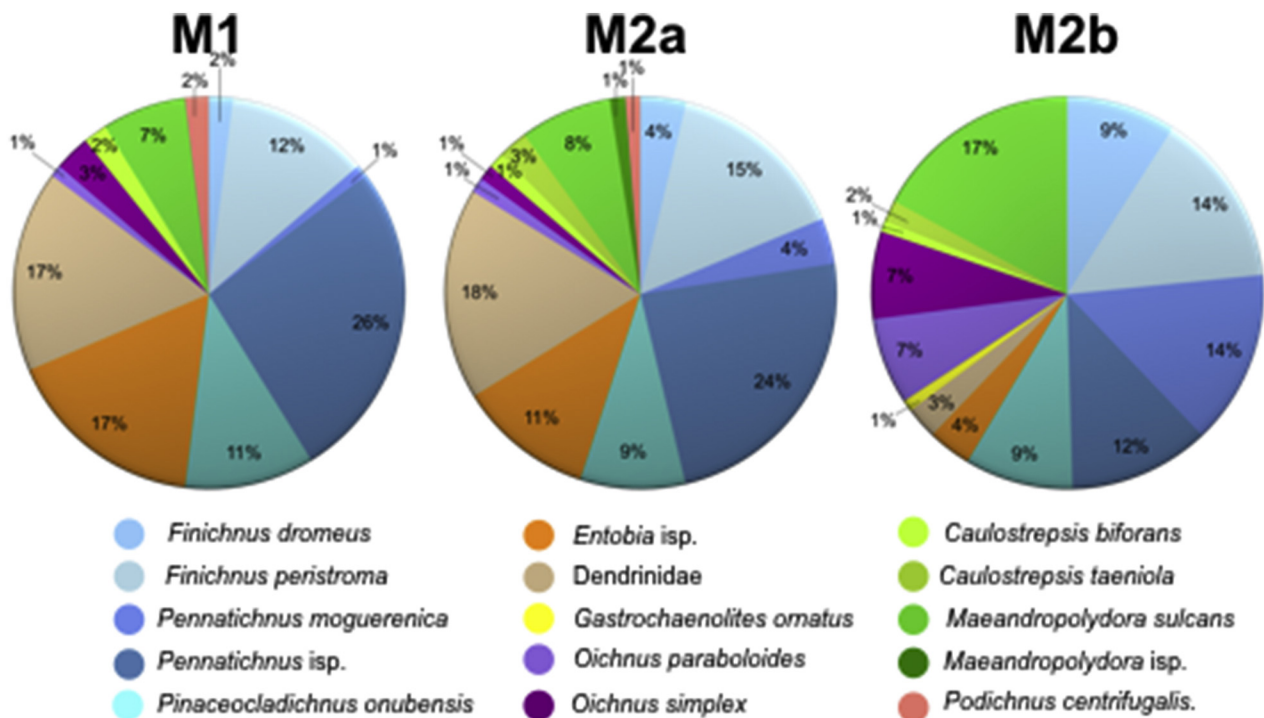


Fig. 3. Ichnodiversity and relative abundance for each sample. Blue: Bryozoans; Orange: sponges; Brown: (?)foraminifera; Yellow: Bivalves; Purple: Predation traces; Green: Polychaetes; Pink: Brachiopods. Sample size: M1 n = 102, M2a n = 80, M2b n = 111

section that is flat-oval or dumbbell-shaped and its apertural grooves are similar to the impression left by the hind limbs of birds. Greater differences exist with *C. taeniola* Clarke, 1908, as this ichnospecies has a well-developed vane separating the limbs, while in *C. cretacea* (Voigt,

1971) the limbs are fused and either without an intermediate wall or with its vestiges preserved as an axial depression.

Ichnospecies *Caulostrepsis taeniola* Clarke, 1908

Material. Elongated U-bent trace (average length 5.75 mm, average

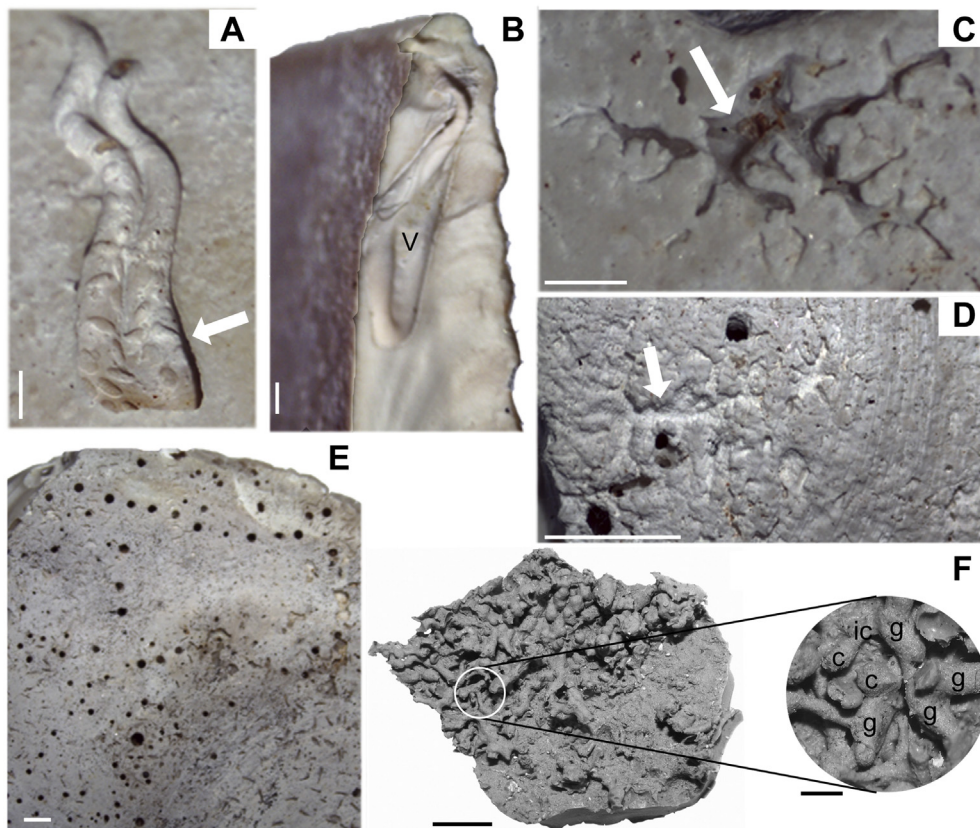


Fig. 4. Bioerosion traces on biogenic substrates from the Monte León Formation. A) *Caulostrepsis biforans* (Gripp, 1967) on the inner surface of a bivalve shell (M2a); see U-shaped gallery bent with limbs joined by a middle wall. Above note *Finichnus* (Taylor et al., 1999) pits (white arrow) that suggests a later colonization of the substrate. B) *Caulostrepsis taeniola* Clarke, 1908 on the fragmented edge of a bivalve shell (M2a); note the presence of the vane (v) between the limbs along the gallery. C–D) Rosetted traces assigned to the Ichnofamily Dendrinidae Bromley et al., 2007 on the outer surface of bivalve shells (M2a); note the system of fine tunnels interconnected by a circular center in C) and by an elongated and irregular center in D) (white arrows). E–F) *Entobia* isp.; E) apertures on the inner surface of a bivalve shell (M1); note the aligned arrangement of the apertures at the periphery that towards the center tends to be irregular; F) Silica cast showing *Entobia* isp. which have irregular galleries (g); note also the chambers (c), and intercameral channels (ic). Scale bar in all figures 0.5 mm.

width 1.4 mm) with limbs (width between 0.5 and 0.9 mm, average 0.7 mm) linked by an intermediate wall towards aperture. Towards the distal end limbs are interconnected by a small and well-developed vane, with an average width 0.25 mm (Fig. 4B); in some cases, the vane shows weathering by surface alteration. The traces are poorly preserved; however, in some of them it is possible to recognize the 8-shaped aperture characteristic of the ichnospecies.

Remarks. The specimens have the enlarged U-bent gallery characteristic of the ichnospecies. The limbs are well defined, not fused like in *Caulostrepsis cretacea*. The presence of a vane distinguishes the ichnospecies from *C. biforans*. On the other hand, the plan view of some specimens is similar to the morphologic variation of *C. contorta* Bromley and D'Alessandro, 1983, from Pliocene deposits in the Bajo del Guadalquivir, Spain (Mayoral, 1991). Due to the difficulty in distinguishing *C. taeniola* from *C. contorta* in plan view –because of the similar morphology of their apertures (Hanken et al., 2012)– the presence of *C. contorta* in some of the specimens studied should not be discarded.

Ichnofamily Dendrinidae Dendrinidae Bromley et al., 2007

Material. Rosetted borings with irregular shape and an open roof aperture (Fig. 4C, D). These traces have a central –even lateral– node from which emerge branched tunnels with variable length, constant diameter, tapering or an anastomosing pattern towards the distal end.

Remarks. Besides the pattern variation of the trace, the rosetted shape of the material here studied agrees with the one described for the Ichnofamily Dendrinidae. Considering the systematic and historic revision by Wisshak (2017), most specimens show affinities with *Pyrodendrina villosa* Wisshak, 2017, due to the open roof aperture and the enlarged node; nevertheless, the presence of other ichnogenera is not discarded.

Ichnogenus Entobia Bronn, 1837

Ichnospecies Entobia isp.

Material. Entobian formed by boxworks of interlocked galleries. The galleries are subcylindrical and irregular with few ramifications. In plan view (Fig. 4E) the apertures are circular (diameter from 0.15 to 0.77 mm, average 0.47 mm) aligned or irregularly arranged. In silicone casts (Fig. 4F) the galleries appear irregular and show thin apophyses. In some parts of the boxwork there are small and irregular knobs joined by small tunnels, which can be interpreted as small chambers joined by intercameral canals.

Remarks. Specimens and silicone casts of the material did not show well-developed chambers like those characterizing *Entobia geometrica* Bromley and D'Alessandro, 1984, *E. ovula* Bromley and D'Alessandro, 1984, and *E. laquea* Bromley and D'Alessandro, 1984. This is reminiscent of *E. megastoma* (Fischer, 1868) in phase C or D sensu Bromley and D'Alessandro (1984) or more mature phases of *E. paradoxa* (Fischer, 1868); this ichnospecies has irregular chambers with amoeboid forms that in mature stages are fused to develop galleries with no chambers. The aperture arrangement suggests that in the studied material there may be more than one ichnospecies.

Ichnogenus Fininchnus Taylor et al., 2013

Ichnospecies Fininchnus dromeus (Taylor et al., 1999)

Material. Shallow and elliptical pits (long axes between 0.16 and 0.33 mm, average 0.20 mm; short axes between 0.09 and 0.14 mm, average 0.11 mm) close to each other, excavated perpendicularly to substrate, showing a uniserial arrangement (Fig. 5A, B).

Remarks. The described traces were assigned to the ichnospecies *Fininchnus dromeus* because of their uniserial arrangement; this characteristic allows differentiating them from *F. tortus* (Rosso, 2008) and *F. peristroma* the arrangement of which is radial.

Ichnospecies Fininchnus peristroma (Taylor et al., 1999)

Material. System of shallow pits (long axes between 0.24 and 0.40 mm, average 0.34 mm; short axes between 0.14 and 0.22 mm, average 0.18 mm) close to each other with a radial arrangement (Fig. 5C, D). The pits near the center are small and elliptical, while towards the periphery they are slightly larger.

Remarks. These traces were assigned to *Fininchnus peristroma*

because of the radial arrangement of the pits, which are smaller in the center of the trace and increase away from it. These traces differ from *F. tortus*, which also has a radial arrangement, by the distal region pits showing a spiral arrangement and with a larger central pit. The traces were not assigned to the ichnogenus *Podichnus* –also showing a radial arrangement– because of the deeper pits that are oblique to the surface of the substrate towards the periphery in *Podichnus*.

Ichnogenus Gastrochaenolites Leymerie, 1842

Ichnospecies Gastrochaenolites ornatus Kelly and Bromley, 1984

Material. Truncated boring inclined 45° with respect to the substrate that produces a sub-circular plan view (major axis 25 mm, minor axis 18 mm; length preserved 16 mm) (Fig. 6A). The base is rounded and ornamented with bioglyphs. No remains of their producer.

Remarks. Despite the incomplete preservation of the specimen, the shape of the base of the gallery and the circular bioglyphs on the inner wall –which are considered as part of the trace and not as the lamination of the substrate– allowed assignment of this trace to *Gastrochaenolites ornatus*. The drop shape of the gallery and the broad and rounded base is similar to that of *G. cluniformis* Kelly and Bromley, 1984, which nevertheless shows a smooth inner wall. Incomplete traces of *G. ornatus* left by erosion like those from Monte León have been recorded by Santos et al. (2012) in basalt rockgrounds in the North Atlantic volcanic islands of Macaronesia.

Ichnogenus Maeandropolydora Voigt, 1965

Ichnospecies Maeandropolydora sulcans Voigt, 1965

Material. Cylindrical and contorted galleries with two apertures (length 4 mm; diameter 0.35 mm) (Fig. 6B). Some morphological variations were observed (Fig. 6C). These include irregularly arranged depressions (sensu Santos et al., 2003). In plan view these depressions can be kidney-shaped, oval or sub-circular (length from 1 to 1.5 mm, average 1.3 mm).

Remarks. The traces differ from *Maeandropolydora elegans* Bromley and D'Alessandro, 1983, because they do not show galleries with paired limbs. On the other hand, the depressions observed were assigned to *M. sulcans* according to the morphological variations proposed by Santos et al. (2003) based on substrate weathering and the tiering of the trace. These depressions differ from the ichnogenus *Renichnus* Mayoral, 1987, because they are not arranged in a row.

Ichnospecies Maeandropolydora isp.

Material. Cylindrical and irregular gallery with more than one aperture. Poorly preserved with limbs not fused. In a sector of the trace the limbs are connected by a vane (Fig. 6D) forming a pouch (length 7.0 mm; width 1.0 mm).

Remarks. This trace was assigned to *Maeandropolydora* due the presence of more than one aperture. The development of the vane suggests it could belong in *M. decipiens* Voigt, 1965; nevertheless, the only poorly preserved specimen precludes any accurate ichnospecific identification.

Ichnogenus Oichnus Bromley, 1981

Ichnospecies Oichnus paraboloides Bromley, 1981

Material. Circular and sub-circular holes (outer diameter 2.0 mm) with a beveled edge and paraboloid cross section (Fig. 6E). The drillings go through gastropod and bivalve shells. In well-preserved shells the inner edge is smooth, and the borehole diameter is less than that of the outer borehole, while in thick shells –or when the surface is very weathered– it becomes difficult to recognize the inner edge.

Remarks. This material was assigned to *Oichnus paraboloides* due to the paraboloid form and to the presence of the beveled and smooth edge. Assignment is doubtful in some specimens due the preservation of the shells. *O. paraboloides* differs from *O. simplex* by the wall of the hole, which in the former ichnospecies is straight and without a beveled edge. It differs from *O. coronatus* Nielsen and Nielsen, 2001 because the hole in our material has a larger diameter and shows no halo.

Ichnospecies Oichnus simplex Bromley, 1981

Material. Cylindrical or subcylindrical holes (diameter 2.0 mm) with smooth walls perpendicular to the substrate surface (Fig. 6F).

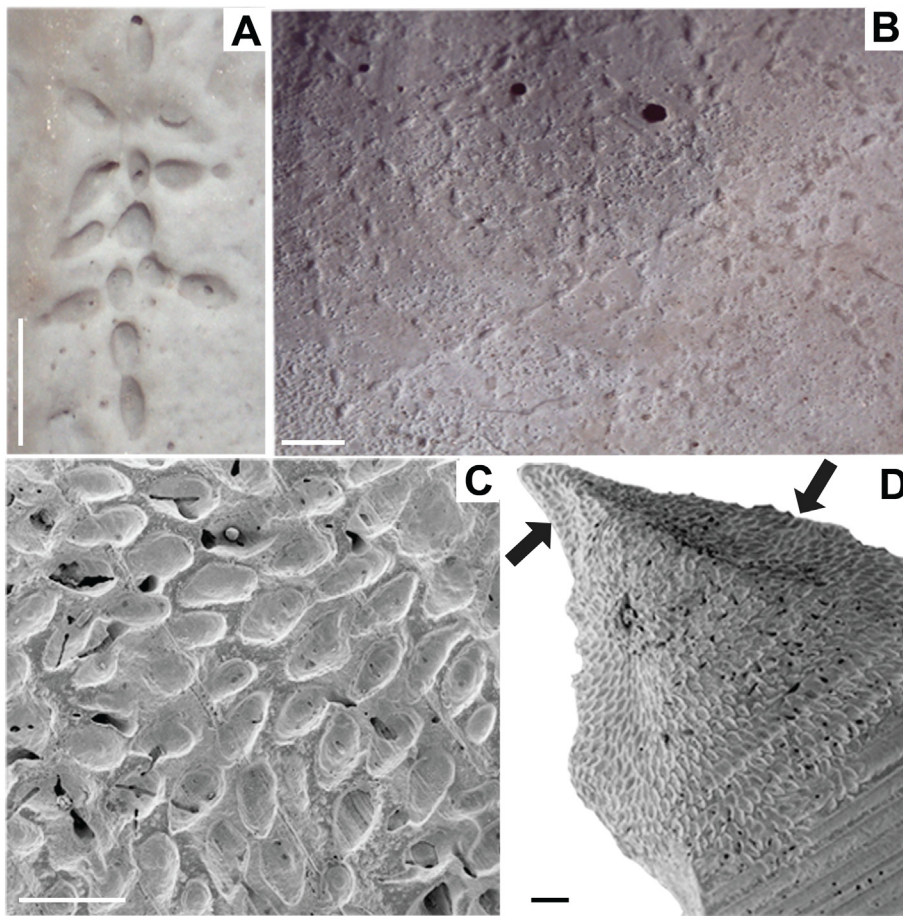


Fig. 5. Bioerosion traces on biogenic substrates from the Monte León Formation. A–B) *Finichnus dromeus* (Taylor et al., 1999); A) on the outer surface of a bivalve shell (M1); B) on the inner surface of a bivalve shell (M2a). C–D) *Finichnus peristroma* (Taylor et al., 1999) SEM images; C) on the outer surface of a bivalve shell (M1); D) same trace; note how the trace colonized the margins that evidenced a previous fragmentation and surface alteration (black arrows). Scale bar in figures A–C) 0.5 mm; in figure D) 1 mm.

When the perforation does not penetrate the substrate, the distal end is shallow and smooth.

Remarks. This trace corresponds to *Oichnus simplex* because its edges are perpendicular to the surface of the substrate and it differs from *O. paraboloides* and *O. ovalis* Bromley, 1993 because it lacks a beveled edge. The origin of the holes is considered biological because they are regular and rounded, without thinned edges as in holes produced by dissolution. In complete or low-fragmentation shells the placement of the trace can be related to a facilitation of access to the tissues of the organisms.

Ichnogenus *Pennatichnus* Mayoral, 1988

Ichnospecies *Pennatichnus moguerenica* Mayoral, 1988

Material. Trace parallel to substrate surface, formed by a thin and elongated principal tunnel (length from 4.2 to 5.5 mm) from which arise alternately, straight or slightly curved subordinated principal conduits (length from 0.09 to 0.29 mm) that are connected with circular or sub-circular primary apertures (long axes between 0.06 and 0.12 mm, average 0.08 mm; short axes between 0.03 and 0.09 mm, average 0.061 mm) (Fig. 7A). The distance between the primary apertures ranges from 0.09 to 0.41 mm (average 0.26 mm) and the distance from the primary apertures to the principal tunnel is between 0.19 and 0.54 mm with an average of 0.34 mm.

Remarks. This trace is included in *Pennatichnus moguerenica* because of the principal tunnel with alternate ramifications that carry circular to sub-circular apertures. The specimens differ from *P. luceni* Mayoral, 1988, because this ichnospecies has drop-shaped primary apertures and subordinate channels slightly curved that together show a virguliform appearance. The material from Monte León shows no affinities with *Iramena Boekschoten, 1970*, because in this ichnogenus the tunnels are arranged in an irregular framework and the primary apertures are kidney-shaped and placed very close to the tunnels. Our

material also differs from *Pinaceocladichnus* by the length of the tunnels and the absence of enlarged chambers.

Ichnospecies *Pennatichnus* sp.

Material. *Pennatichnus* parallel to the substrate surface, formed by a thin and long principal tunnel with the substrate surface, formed by a thin and long principal tunnel with oval chambers (long axes from 0.136 to 0.351 mm, average 0.225 mm; short axes from 0.045 to 0.109 mm, average, 0.071 mm) arranged alternately at an angle ranging between 30° and 72° (average 52°) (Fig. 7B).

Remarks. These traces are assigned to *Pennatichnus* because of the alternate arrangement of the chambers along the sides of the main tunnel. Nevertheless, they differ from *P. luceni* and *P. moguerenica* because they do not have subordinate principal conduits connecting the primary apertures with the principal tunnel.

Ichnogenus *Pinaceocladichnus* Mayoral, 1988

Ichnospecies *Pinaceocladichnus onubensis* Mayoral, 1988

Material. System of shallow thin tunnels (diameter between 0.006 and 0.020 mm, average 0.014 mm) parallel to substrate; the tunnels have a symmetrical bifurcation that results in secondary tunnels (diameter 0.013 mm) (Fig. 7C). Both kinds of tunnels carry circular or sub-circular primary apertures (diameter from 0.014 mm to 0.044 mm, average, 0.030 mm) connecting with elongated and narrow chambers (length between 0.20 and 0.33 mm, average 0.26 mm; width between 0.030 and 0.090 mm, average 0.060 mm) (Fig. 7D).

Remarks. The traces were identified as *Pinaceocladichnus onubensis* because of the regular bifurcation of the tunnels and the presence of elongated chambers. Although this trace has tunnels like those in ichnospecies of *Iramena*, in *Iramena* the tunnels are arranged in an irregular framework and the primary apertures are kidney-shaped and placed very close to the tunnels. In the studied material, the tunnels sometimes appear highlighted due surface alteration. On the other hand, in some parts of the substrate it may become difficult to recognize

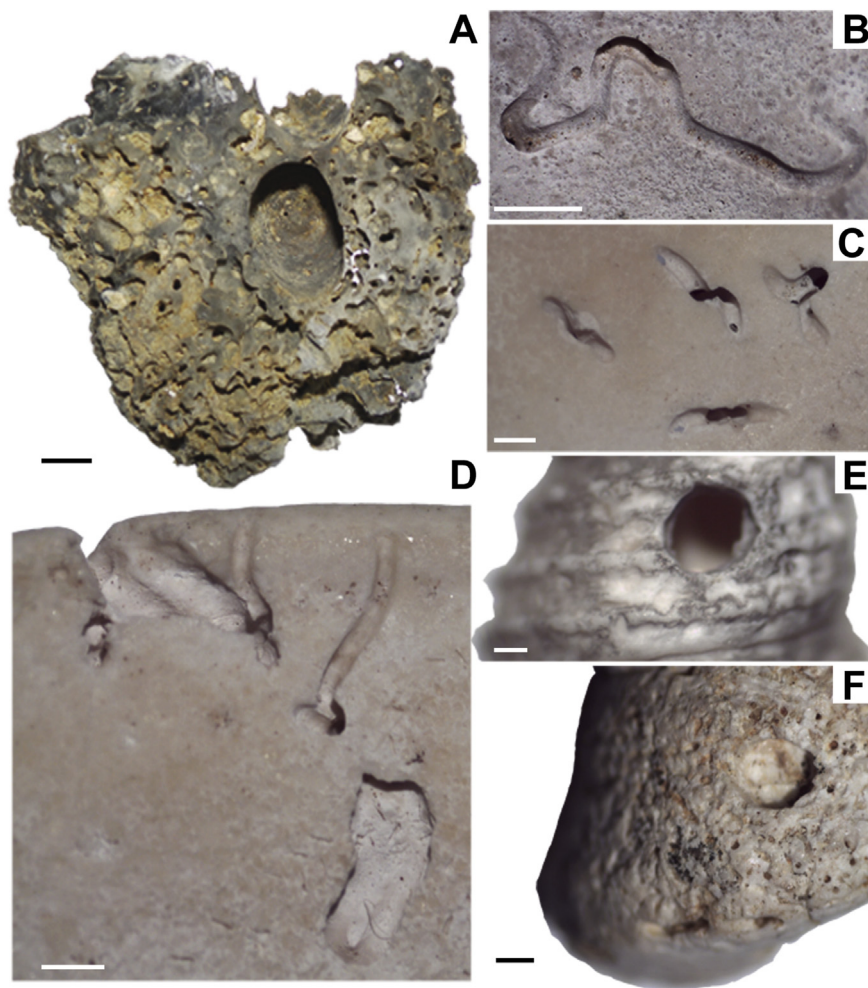


Fig. 6. Bioerosion traces on biogenic substrates from the Monte León Formation. A) *Gastrochaenolites ornatus* Kelly and Bromley, 1984 on a valve of “*Ostrea*” *hatcheri* Ortmann, 1897 (M2b). B–C) *Maeandropolydora sulcans* Voigt, 1965; B) on the inner surface of a bivalve shell (M2a); note the contorted gallery with two apertures; C) Possible morphologic variations of the trace (sensu Santos et al., 2003). D) *Maeandropolydora* isp. on the inner surface of a bivalve shell (M2a); note the subsequent colonization by *Pennatichnus* isp. near and on the limbs. E) *Oichnus paraboloides* Bromley, 1981 in a turritellid shell (M1). F) *Oichnus simplex* Bromley, 1981 in a gastropod shell (M2b); note the flat base related with a failed attack. Scale bar in figures A) 10 mm; in figure B–F) 1 mm.

the trace because it can be overlapped by other traces.

Ichnogenus *Podichnus* Bromley and Surlyk, 1973

Ichnospecies *Podichnus centrifugalis* Bromley and Surlyk, 1973

Material. Set of circular or sub-circular pits (diameter between 0.020 mm to 0.030 mm, average 0.022 mm) that penetrate the substrate obliquely and show a radial arrangement (Fig. 7E, F).

Remarks. The material from Monte León is assigned to *Podichnus centrifugalis* due to the circular shape of the pits and their radial arrangement. The traces differ from *P. perpendicularis* Robinson and Lee, 2008 by the shape of the pits that in this ichnospecies are extended laterally to form curved grooves. Regarding the pit arrangement, it differs from that of *P. conicus* Santos and Mayoral, 2014 (in Santos et al., 2014) which shows a radial but asymmetrical arrangement. Our material cannot be identified either with *P. obliquus* Robinson and Lee, 2008, as in this ichnospecies the peripheral pits tend to be very separate from each other.

5.2. Diversity of sclerobionts according to the taphonomic characteristics of the substrate

The substrate in which bioerosion traces were recorded is biogenic, namely gastropod and bivalve shells. In each sample, the substrate as a whole shows particular taphonomic signatures (Fig. 8). Predominant in samples M1 and M2a are shells with high bioerosion, fragmentation and surface alteration degree. Conversely, even if bioerosion is high in M2b, shells with low to moderate fragmentation and surface alteration are predominant. Individually shells can be assembled –according to their taphonomic features– into different groups that are present in

different proportions in each sample, also showing a distinctive distribution and diversity of sclerobionts.

The dominant group in both shell concentration is characterized by specimens with poor size selection and high fragmentation, surface alteration and bioerosion. The shells that share these taphonomic features are infaunal and semi-infaunal bivalves and gastropods belonging to the families Hiatellidae, Veneridae and Turritellidae; bivalves predominate in samples M1 and M2a, while turritellids predominate in sample M2b. The fragments of bivalve shells measure from 5.66 to 56 mm (in this work we only considered material retained in 3¹/₂ sieve; see Methods), with an average of 19 mm. The surface is chalky and weathered; the ornamentation looks diffuse and in some specimens is completely lost. The preserved ventral margins are smooth and weathered too, while the edges produced by fragmentation are rounded or sharp. *Pennatichnus* and *Entobia* are predominant. On the other hand, turritelliform shells show moderate to high fragmentation, the preserved apices are rounded while the bases of the shells, the apertures and the columella are fragmented. The surface is chalky, the spiral cords appear rounded and diffuse. In these shells the most abundant traces are *Caulostrepsis*, *Finichnus*, *Maeandropolydora* and *Pennatichnus*.

Another distinct group is composed of well-size-sorted and well-preserved bivalve shells of *Pleuromeris* Conrad, 1867 (length < 10 mm) showing low fragmentation, surface alteration and bioerosion. It is present in the three samples although it is scarce. The ornamentation of the valves is well-preserved, the shell surfaces are polished; edges are smooth and continuous; the hinge teeth are well preserved. Bioerosion traces are scarce and only occur on the external side of the valves and are represented by the ichnogenera *Finichnus*, *Oichnus* and *Podichnus*.

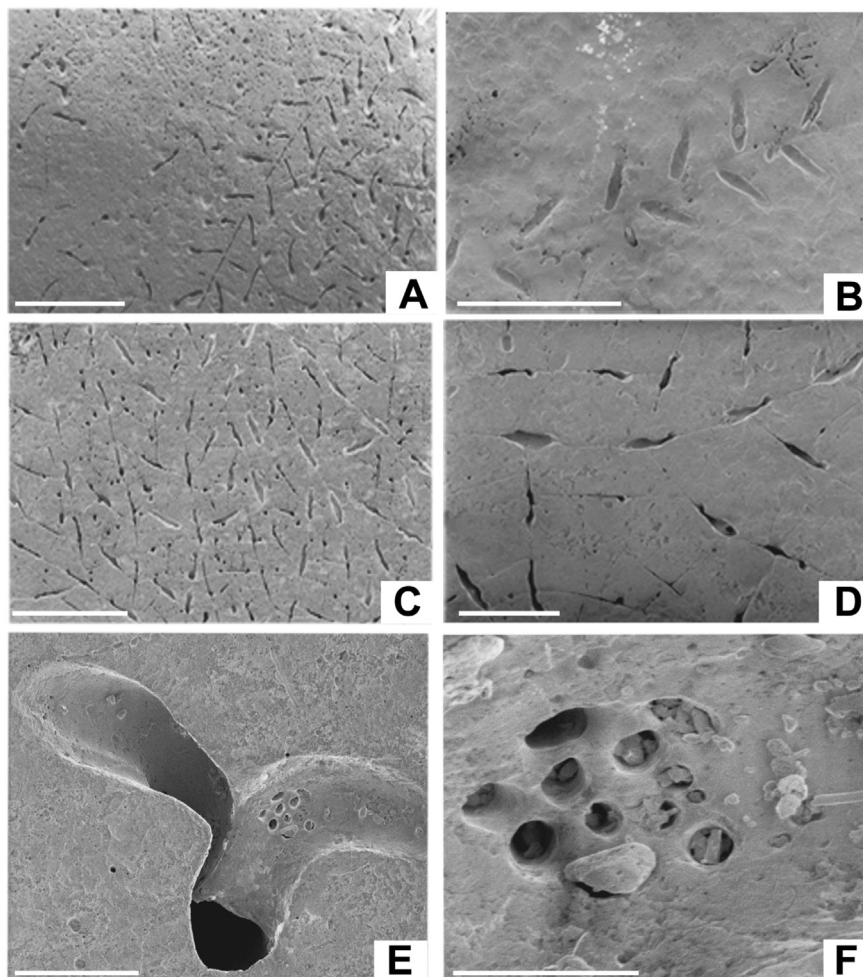


Fig. 7. Bioerosion traces on biogenic substrates from the Monte León Formation. A) *Pennatichnus moguerenica* Mayoral, 1988, SEM image on the inner surface of a valve (M1); note the thin and elongated principal tunnel and the alternated branching of the subordinated principal conduits; B) *Pennatichnus* isp., SEM image on the inner surface of a valve (M2a); note the absence of the subordinate principal conduits. C–D) *Pinaceocladichnus onubiensis* Mayoral, 1988 on the inner surface of a valve (M1), SEM images; C) system of fine primary tunnels branching into secondary tunnels; also note the elongated and narrow cavities; D) close up of C) showing the primary and subcircular apertures that are connected to the principal cavities. E–F) *Podichnus centrifugalis* Bromley and Suriyk, 1973, SEM images; E) above a trace of *Maeandropolydora sulcans* Voigt, 1965 on the inner surface of a valve (M2a). F) close up of E); note that the pits are oblique to the substrate. Scale bar in figures A–C) 1 mm; in figures D–E) 0.5 mm; and in figure F) 0.25 mm.

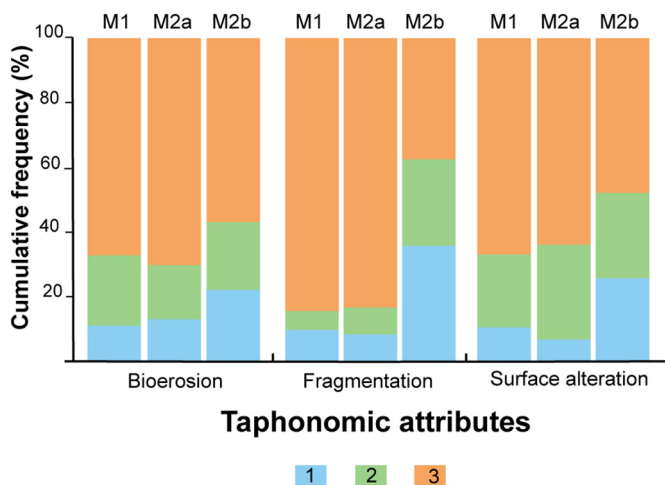


Fig. 8. Taphonomic attributes in each of the three studied samples. 1 (blue), low; 2 (green), moderate; 3 (orange), high.

The calcitic composition of the shell and its high taphonomic indexes allow us to consider separately a singular fragment, 85 mm in diameter, of *Ostrea hatcheri*, even if only one specimen is available. The specimen with rounded edges and showing high dissolution comes from sample M2b. Bioerosion is high, affecting the entire surface and shows a considerable richness that includes traces of *Entobia*, *Gastrochaenolites* and *Maeandropolydora*. The presence of encrusters such as bryozoans and barnacles is also remarkable.

The last group is composed of gastropod (Muricidae, Volutidae, Calliostomatidae, Trochidae and Struthiolariidae) specimens with a good to moderate size-selection and low fragmentation and low to moderate surface alteration. Most of the specimens have a continuous ornamentation and a porcellanaceous texture, while in a few the ornamentation is rounded and weathered and the appearance is chalky. It appears in both concentrations in a moderate proportion but in sample M2b the preservation is better than in the other samples. Bioerosion is moderate and the predominant traces are *Finichnus*, *Pennatichnus* and *Oichnus*.

5.3. Sclerobiont selectivity for substrate surface

When the presence of the traces in both surfaces of the substrate were independently assessed, it became clear that the preference for both or only one of the surfaces of the substrate varied for the different producers according to the samples (Table 2). In samples M1 and M2b, traces produced by bryozoans and polychaetes (Table 1) showed a significant preference for colonizing only one of the surfaces. Dendri-form traces, possibly produced by forams (Table 1), showed a preference to colonize only one surface of the substrate in sample M1. Finally, entobian traces produced by sponges (Table 1) did not show significant preference in any of the samples studied (Table 2).

On the other hand, when assessing –for each producer in each sample– if there was any preference to colonize the internal or the external side of the shells (Table 3), only bryozoans and polychaetes from sample M2b showed a highly significant preference for the external side with a p-value < 0.001.

All producers taken together for each of the three samples revealed

Table 2

Exact Goodness-of-Fit Test that evaluates independently whether each trace producer showed preference to colonize both surfaces of the substrate or only one of them. The values were adjusted using the Bonferroni method to detect false positives or negatives.

Producer	p-value	Confidence intervals	Probability	p-value Bonferroni
M1 (one-both sides)				
Bryozoans	< 0.001	0.617–0.862	0.754	0.001
Foraminiferans	0.002	0.635–0.985	0.882	0.009
Polychaetes	0.039	0.517–0.997	0.888	<u>0.156</u>
Sponges	0.343	0.347–0.933	0.700	1.000
M2a (one-both sides)				
Bryozoans	0.2912	0.432–0.736	0.590	1.000
Foraminiferans	0.1796	0.418–0.916	0.714	0.718
Polychaetes	0.1094	0.443–0.974	0.800	0.437
Sponges	0.5078	0.074–0.700	0.333	1.000
M2b (one-both sides)				
Bryozoans	< 0.001	0.849–0.982	0.9384	< 0.001
Foraminiferans	0.250	0.292–1.000	1.000	1.000
Polychaetes	< 0.001	0.845–1.000	1.000	< 0.001
Sponges	1.000	0.067–0.932	0.500	1.000

False positive p-value is in bold and underline.

Table 3

Exact Goodness-of-Fit Test that evaluates independently if each trace producer showed preference to settle in a particular surface of the substrate (inner or outer). The values were adjusted using the Bonferroni method to detect false positives or negatives.

Producer	p-value	Confidence intervals	Probability	p-value Bonferroni
M1 (internal-external surface)				
Bryozoans	0.153	0.458–0.772	0.625	0.615
Foraminiferans	0.118	0.077–0.551	0.266	0.474
Polychaetes	1.000	0.157–0.842	0.500	1.000
Sponges	0.125	0.003–0.578	0.142	0.500
M2a (internal-external surface)				
Bryozoans	0.557	0.369–0.766	0.576	1.000
Foraminiferans	0.118	0.077–0.551	0.266	0.474
Polychaetes	0.289	0.349–0.968	0.750	1.000
Sponges	0.250	0.292–1.000	1.000	1.000
M2b (internal-external surface)				
Bryozoans	< 0.001	0.171–0.408	0.278	0.002
Foraminiferans	1.000	0.008–0.905	0.333	1.000
Polychaetes	< 0.001	0.001–0.228	0.045	< 0.001
Sponges	0.500	0.158–1.000	1.000	1.000

Significant p-values (< 0.05) are in bold.

Table 4

Fisher test that evaluates independently if producers as a whole showed preference to colonize both surfaces of the substrate or only one of them.

Producer	M1 Fisher test		M2a Fisher test		M2b Fisher test	
	Both sides	One side	Both sides	One side	Both sides	One side
Bryozoans	13	40	18	26	4	61
Foraminiferans	2	15	4	10	0	3
Polychaetes	1	8	2	8	0	22
Sponges	10	7	6	3	2	2
	p-value	0.010	p-value	0.187	p-value	0.027

that –using a Fisher test (Table 4)– in the first shell concentration (sample M1) producers showed a significant preference to colonize only one of the shell surfaces (p-value < 0.05). In the second concentration, the samples rendered different results; in sample M2a no preference to colonize the substrate surface was shown whereas the p-value was

significant in sample M2b (p-value < 0.05).

6. Discussion

6.1. Sclerobiont palaeobiology and substrate surface selectivity

The studied traces were produced mainly by bryozoans in both shell concentrations, and these traces are also the ones showing the highest ichnodiversity (three ichnogenera and four ichnospecies). These are followed by sponge and (?)foraminifera traces in M1 and M2a and by polychaete traces in M2b (Fig. 3).

Finichnus is considered a domichnia produced by different species of cheilostome bryozoans of the families Membraniporidae, Electridae, Cribrilinidae, Hippothoidae, Microporellidae and Romancheinidae (Taylor et al., 1999). This ichnogenus has been recorded mainly on aragonitic and calcitic shells of gastropods and bivalves. On the other hand, the ichnogenera *Pennatichnus* and *Pinaceocladichnus* are considered as domichnia too but produced by ctenostome bryozoans. Mayoral (1988) suggested that the perforation model of *P. moguerenica* is related to the perforations produced by the extant ctenostome *Spathipora occidentalis* Pohowsky, 1978. In this model, elongated cavities correspond to the individual zooids that are connected to a stolon network by means of a small peduncle. Likewise, Mayoral (1988) pointed out that *Pinaceocladichnus* shows similarities with the perforations produced by extant *Immergentia* spp. Casadío et al. (2007) described *Pinaceocladichnus* on shells of the gastropod *Antarctodarwinella ellioti* Zinsmeister, 1976, from the Eocene La Meseta Formation in Seymour Island, Antarctica, stating that the traces show similarities with the perforations produced by the genus *Terebripora* d'Orbigny, 1847.

The abundance and diversity of bryozoan traces in the three samples is remarkable (Fig. 3). Because of their current distribution and the diversity of forms that bryozoan colonies show, it has been suggested that they can be used as proxies of palaeoenvironmental conditions. In this sense, an abundant record of these invertebrates is a good proxy of low stress conditions (Smith, 1995). According to this, it is possible that the shells of both concentrations of the studied section were deposited –before final burial– in a shallow marine environment with low to moderate energy favoring the presence of nutrients and in which sedimentation rate was low. The abundance of these traces also could be related to the exposure time of the substrate at the water-sediment interface. In this sense it has been observed that these invertebrates show a trend to settle preferably on ephemeral or moderately long-lived stable substrates (shells and cobbles among others) rather than on permanent ones on which bryozoans may lose ground to competitors such as sponges, ascidians or algae (Smith, 1995). Substrate surface selectivity varies between the two shell concentrations (Table 2). In the first concentration (sample M1) traces show a preference for colonizing one side of the substrate; however, no preference was observed for the internal or external surface of the shell. In the second shell concentration the selectivity for any side of the substrate showed differences between the two samples considered (M2a and M2b) (Table 2). In M2a the bryozoan traces distribution on the substrate was random, while in M2b they showed a preference not only for one side but particularly for the external one (Table 3). This highly significant preference for the external surface in M2b could be related to the fact that this sample includes mainly infaunal and semi-infaunal gastropod shells, which when exposed to the interface show a limited available surface because of the fewer inner regions exposed (i.e. part of the last whorl, inner lip and columella). In contrast, sample M2a contains mainly whole valves and fragments of bivalves; in this case both sides of the shells could be exposed after death, disarticulation and fragmentation.

The traces produced by polychaetes correspond to the ichnogenera *Caulostrepsis* and *Maeandropolydora*. These domichnia traces reflect two different modes of substrate penetration (Bromley and D'Alessandro, 1983) and are characterized by at least one aperture towards the water

column, a feature that suggests that they were produced by filtering organisms (Wilson, 2007). Extant *Caulostrepsis* is produced mostly by the genus *Polydora* (Bosc, 1802 (Bromley, 2004); during the drilling process the worm dissolves the shell by means of chemical secretions and physical strategies using their falcate notochaetae to form the U-shaped gallery with a central island filled with detritus (Botelho de Souza et al., 2017). Bromley (1978) suggested that *Lysidice ninetta* Audouin and Edwards, 1833 also produces this trace. *Maeandropolydora* also has been attributed to the drilling activity of polychaetes moving irregularly at different levels below the substrate and thus promoting the morphological diversity observed in this trace (Santos et al., 2003).

The traces produced by polychaetes showed a preference to colonize one side of the substrate in M1 and M2b (Table 2). In sample M1 the preference for the internal or external sides was indistinct (Table 3), suggesting that the substrate that form it was moved (even within the deposit), thus allowing exposure of both sides of the substrate to the water column. In contrast, in M2b there is a highly significant preference to colonize the external surface of the shells (Table 3). As with the bryozoan traces, this result could be influenced by the abundance of gastropod shells in which the space that could be used for settlement on the internal surface is restricted.

Entobian traces are produced by clionid sponges that penetrate calcareous substrates to build complex systems of interconnected chambers or galleries, always with multiple connections to the outside water. Thus, the extensive network of small holes on the substrate surface favours water-filtration (Wilson, 2007). The role of these bioeroders in the marine communities has been widely studied since the past century (e.g. Volz, 1939; Bromley, 1970; Rützler, 1975), mainly in reef environments. Different experimental methods revealed that their diversity and abundance is influenced mainly by the nature, homogeneity and availability of hard substrates. Physical factors such as sedimentation rate, luminosity, water energy, and ecological factors such as the presence of other encrusters and predators have an important influence in the growth and colonization pattern of the sponges (Bromley and D'Alessandro, 1984).

Sponge traces are less abundant than bryozoan traces in our samples, especially in sample M2b. This could be related to competitive interactions for space or to the type of substrate. In sample M2b thick fragments of bivalve shells are far less common than in the other two samples. In all three studied samples this ichnogenus shows no preferences to colonize a particular surface of the substrate (Table 2).

Other abundant traces in the fossil concentrations at Cabeza de León are dendritic and rosette borings included in the ichnofamily Dendrinidae as established by Bromley et al. (2007). These traces are considered as domichnia structures, but the identity of the producers remains speculative and subject to debate; yet, the most likely producers appear to be excavating micro-sponges and endolithic foraminiferans (Bromley et al., 2007; Buatois et al., 2017; Wisshak, 2017). It has been reported that forams can colonize different organic substrates such as shells, bryozoans, crustaceans, other forams, corals and calcareous algae with different purposes, e.g. parasitism, protection, feeding or as carbonate source to build their test (Véneç-Peyré, 1996). Although the bioerosion rate of these protists has not been estimated or studied as extensively as is the case of other bioeroders, around 20 species of this group are known to have this life habit. The earliest studies about these organisms were focused on parasitism and on the host-endobiont relationship. Currently, the impact that the activity of these organisms has in the destruction of hard substrate began to be recognized because even if their traces are small they weaken the substrate and render it vulnerable to other erosive processes. Also, the construction of microscopic cavities on the surface of unoccupied biogenic substrates facilitates the recruitment of other bioeroders. Thus, bioeroding forams could favor the development of hard substrate communities (Hutchings, 1986; Véneç-Peyré, 1996).

Among the samples studied, we observed that only in sample M1 Dendrinidae showed a preference to colonize one surface of the

substrate (Table 2), yet not showing a preference for the internal or external surface (Table 3). As in the case of bryozoans and sponges, this can reinforce the idea of substrate mobility along its biostratigraphic history.

Oichnus is classified as praedichnia and is produced by durophagous organisms; it is scarce in our fossil concentrations. Different mechanisms of subjugation exist in durophagy, drilling being the most specialized (Vermeij, 1987). Although nowadays these traces are produced mainly by muricids and naticids, it is risky to assume the same producers or the same ethological category throughout the fossil record (Bromley, 1981; Kowalewski, 2002). These traces could be produced by different organisms including 14 groups of invertebrates (e.g. nematodes, gastropods and octopods), parasites or predators. Gastropod boreholes assigned to naticids have been previously reported from shells collected in the Monte León Formation (Signorelli et al., 2006), where the presence of gastropods referable to the families Naticidae, Muricidae and Buccinidae is common. It may be possible that they produced the traces studied here, although the low preservation potential of other predators and parasites should be considered too. The ichnological identification of these traces was based on the emended diagnosis by Wisshak et al. (2015), which include those perforations that bore completely through the substrate and those that do not penetrate it completely and are considered as failed attacks.

Podichnus is very rare in both shell concentrations. This fixichnia trace is produced when brachiopod pedicles etch into a carbonate substrate. Robinson and Lee (2008) described three types of traces that are made by the rootlets and the papillae of the pedicles during etching, moreover these authors attributed the traces to different orders and suborders of brachiopods. Terebratulidae have been reported by Parras et al. (2012) in the Monte León Formation and collected by us when sieving material from the Cabeza de León section in a mesh size $< 3^{1/2}$ (see Methods). *Podichnus* traces were not included in the statistic test due to the low number of specimens.

Finally, *Gastrochaenolites* was recognized in a sole highly altered specimen that preserved only the base of the gallery. This domichnia trace is produced by endolithic bivalves of the families Pholadidae, Gastrochaenidae and Hiattellidae, the shells of which show adaptations allowing them to penetrate hard substrates. This ichnogenus was not considered in the test of selectivity because only one specimen was available.

Statistical tests for substrate surface selectivity represent mainly the specimens with high taphonomic indexes and an infaunal or semi-infaunal life habit because their high proportion in the two shell concentrations. On bivalve shells –that dominate in samples M1 and M2a– the colonization of both sides could be eased by their mobility and hydrodynamic behavior, which facilitated both sides of the shell and even the margins becoming exposed to the water column at different moments. This model may be similar to that observed in conglomerates (Siggeud et al., 2000; Pineda-Salgado et al., 2015) but at a smaller scale. In gastropods –more abundant in sample M2b– the morphology of the shells was a crucial factor during attachment of the sclerobionts because access to the internal surface is limited to some organisms.

6.2. Sclerobionts and taphonomic history of the colonized substrate

The presence of different taphonomic signatures in shells of the studied concentrations indicates that these concentrations went through diverse biological and sedimentary processes before final burial.

The poor shell preservation and the fact that they belong mostly to infaunal mollusks, suggest that the dominant group in both concentrations is formed mainly by parautochthonous elements. The poor size-sorting, high fragmentation and chaotic or concordant orientation together with the complete disarticulation of all the bivalves suggest transport. In the lower part of the second shell concentration, the concordant convex-up orientation of the shells suggests the presence of

long term unidirectional or oscillatory currents, or else storm flows (Fürsich and Oschmann, 1993). The high surface alteration –including rounded edges– could be related to long-term transportation. However, it can suggest also that the shells were exposed at the water-sediment interface at different stages of their taphonomic history. Bioerosion associated with the exposure of the material at the interface may also contribute to surface alteration due to abrasion and dissolution exerted by sclerobionts on the substrate during settlement. On the other hand, turrillid shells could have been used by hermit crabs, as occurs in recent littoral environments (e.g. Manjón-Cabeza and García-Raso, 1999). It was experimentally demonstrated that it is possible to recognize the hermit gastropod shells based on the sclerobionts and their colonization patterns on the shells (Walker, 1988, 1989, 1992). Yet, there is no evidence at present to confirm that this biological process occurred in turrillid shells in our samples. Bryozoan traces located at the aperture of the shell are not always a proxy of pagurization, except when colonization occurs in a particular way (Walker, 1992) and this was not the case in our material as the traces were located along the entire shell surface of gastropod. Although crustaceans have been recorded in the Monte León Formation (Crawford et al., 2008), these do not include pagurids.

Excellent preservation of the *Pleuromeris* specimens, a seminfaunal or asiphonate infaunal bivalve, suggests an autochthonous origin for them. The good size-sorting of these specimens cannot be considered as a proxy because only the material retained in the 5.660 mm was considered, and in smaller meshes (1.190 mm and 0.710 mm) the abundance of *Pleuromeris* valves is considerable. Low bioerosion together with other taphonomic attributes suggest that exposure of these shells at the water-sediment interface was not prolonged.

The sole fragment of the large oyster identified suffered extreme fragmentation, bioerosion and surface alteration, so much that it becomes extremely difficult to identify which is the internal and which the external surface. These characteristics also suggest a prolonged transport by water currents or a long exposure at the water-sediment interface, possibly under wave action. Thus, it seems highly probable that this specimen is allochthonous. Bioerosion is high and could have occurred while the oyster was alive or else postmortem. In this sense, the gregarious habit of ostreids and their prolonged exposure to the interface together with their shell characteristics, offers an ideal substrate for the attachment of different sclerobionts. After death, oyster shells can be an ideal substrate for marine hard substrate communities too.

Finally, the good preservation of epifaunal gastropods shells –including low to moderate fragmentation, surface alteration and bioerosion– suggests that they could be autochthonous. Due to the life habit, it is difficult to identify whether bioerosion occurred during life or post-mortem.

The taphonomic and palaeobiological attributes of the studied specimens leads us to consider that the two shell concentrations have a mixed origin and belong to the biogenic-sedimentologic categories (sensu Kidwell et al., 1986) constituted by autochthonous and parautochthonous-allochthonous elements. In these kinds of fossil concentrations, hard parts act like a coarse-texture substrate in an environment that was characterized mainly by the presence of fine-grained sediment. Thus, the new colonizers, their skeletal remains and their traces are different from the initial fossil concentration (Kidwell et al., 1986).

The erosive base, dense packing, variable size sorting (good to poor), convex-up concordant or chaotic orientation with direct gradation, together with the variable taphonomic signatures recognized in both concentrations, reflect a gradual mixture and mechanic destruction of the original communities. These traits suggest also the action of short-term and high energy events such as storm flows as responsible of the final shell concentrations. The high surface alteration of most of specimens, including the high abrasion and rounded edges, indicate that the shells were reworked by wave action before the final process of

concentration by storms. On the other hand, the taphonomic attributes of some specimens (e.g. *Pleuromeris*, epifaunal gastropods) reflect less reworking and short periods of transport. These taphonomic signatures were later modified by biological factors including mainly bryozoan bioerosion in a shallow environment with a low sedimentation rate. Thus, the final biogenic-sedimentologic shell concentrations include elements that underwent quite different taphonomic histories.

7. Conclusions

In the two fossil concentrations in the Monte León Formation that we studied, we recognized fifteen ichnotaxa belonging in the ethological categories domichnia, praedichnia and fixichnia. The dominant trace producers were bryozoans followed by sponges, (?)foraminifera and polychaetes. When the distribution of the traces on the surface of the shells were studied, traces in samples M1 and M2b showed a significant preference to occupy only one of the surfaces of the substrate. Only in M2b there was a preference for the external surface, probably explained by the abundance of gastropod shells. On the other hand, the abundance of fragmented bivalve shells in sample M2a contributed towards a random distribution of the traces on both shell surfaces.

Besides the high bioerosion, dissimilarity in other taphonomic attributes allowed to identify that the concentrations are of mixed origin (biogenic-sedimentologic) and include elements with different taphonomic histories. Dominant specimens are parautochthonous and allochthonous and have signatures of reworking and transport before final burial, while some other specimens (e.g. *Pleuromeris* and epifaunal gastropods) show less transport and reworking. The mixture of these elements during final deposition could be the result of short-term high-energy events such as storms. The high abundance of traces produced by bryozoans in both shell concentrations suggests that before final burial shells were exposed in a shallow marine environment with low to moderate energy, low sedimentation rate and abundant nutrient availability.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2018.09.029>.

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